2, On the Temporal Arches of the Reptilia.

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(Text-figures 1–4.)

In the last thirty years most of the attempted classifications of the Reptilia have been based on the structure of the temporal arches. It is generally agreed that all the later reptiles have descended from a Lower Permian ancestor or ancestors that had a roofed temporal region, and the arches found in later forms have manifestly resulted from a fenestration of the ancestral roof.

Many reptiles have a temporal region which has resulted from one opening in the ancestral roof: others have a temporal region in which two openings have been formed. If all later reptiles could be classed into those with two temporal openings, those with only one, and those with none, and if we could be quite certain that the pair of openings in those reptiles with two and the single opening in those with one were homologous the classification would be a very easy matter. Unfortunately, we have a number of groups where the nature of the temporal region is not quite clear, and at present there is no general agreement as to the origin or affinity of these groups.

There is almost universal agreement that at least all the later reptiles with two temporal openings are closely related and form a natural group to which the name Diapsida has been given by Osborn. In this group we have the Dinosaurs, Crocodiles, Phytosaurs, Pterosaurs, Rhynchosaurs, Rhynchocephalians, and the primitive order I added a few years ago, the Eosuchia. There is also general agreement that the Mammal-like reptiles with a single temporal opening form a second natural group. But we are left with the following important orders, concerning which there is doubt—Ichthyosauria, Plesiosauria, Placodontia, Chelonia, and Lacertilia.

The Ichthyosaurs, Plesiosaurs, and Placodonts agree in having a single temporal opening. The doubt is whether this single opening is homologous with the single opening in the temporal region of the Mammal-like reptiles. The very large majority of morphologists are of opinion that it is—I think it is not.

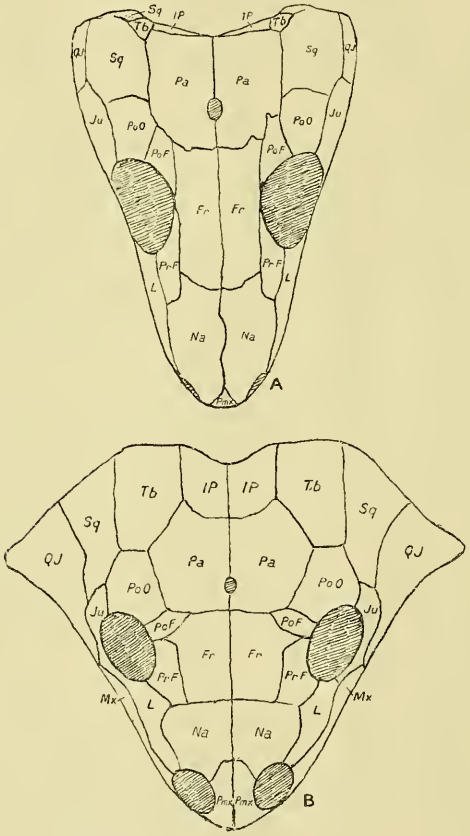
The Chelonians have a temporal region which looks as if it had never been fenestrated at all, but merely in many types encroached on from behind or below. Some hold that the temporal region is still a simple roofed one. But there are at least two other possibilities. The Chelonians may be derived from an ancestor which had one temporal opening like the Plesiosaur, or two as in *Sphenodon*, where the openings had become secondarily closed, or they may have originated from an

ancestor which had a single temporal opening and whose immediate descendants lost the posterior squamoso-parietal bar.

The lizards, though held by most to be derived from a two-arched ancestor like *Youngina* by the loss of the lower bar, are held by others to be the modified descendants of ancestors which never had more than one temporal opening.

Some discussion of these debatable points may not be unprofitable.

Text-figure 1.



A. Skull of *Captorhinus aguti* (Cope).
B. Skull of *Pareiasaurus* sp. After Watson.

Cope, Smith Woodward, and all later writers have taken as the primitive reptilian condition of the temporal region a roofed temporal region such as is seen in the Labyrinthodonts or in one of the early Cotylosaurs, such as *Pantylus* or *Labidosaurus* or the

allied *Captorhinus*. But whether or not the reptiles have been derived from a Labyrinthodont or even a *Seymouria*-like ancestor need not at present concern us, as we have a temporal roof in *Pantylus* primitive enough to have been the origin of all the later types of temporal regions seen in higher reptiles. Those who believe that in many later reptiles, such as *Ichthyosaurus*, *Pleurosaurus*, and others, we still have a well-developed supratemporal element, must necessarily derive them from an ancestral type such as we have in *Pantylus*, where the supratemporal is still preserved. Personally, I am of opinion that all the so-called supratemporal bones in later reptiles are really tabulars, that the supratemporal was very early lost never to reappear, and that a temporal region such as we have in *Captorhinus* gives us a better idea of the ancestral reptilian temporal roof than any other well-known animal.

It is, of course, a point which might be debated at considerable length whether it is the tabular which is lost and the supratemporal retained in the primitive Diapsids or the supratemporal lost. The evidence is not as convincing as one would desire; but, as I am showing elsewhere, there seems good reason to believe that the upper bone in the temporal region of the lizard is the tabular, and in the most lizard-like of the Cotylosaurs such as *Procolophon* it is certainly the tabular that is retained and the supratemporal lost, so we are probably justified in concluding that except in a few primitive Cotylosaurs such as *Pantylus* and *Diadectes* a supratemporal is never found in reptilian skulls.

Captorhinus, though it has all the ancestral elements of the temporal region and only those that are met with in most later reptiles, is considerably specialised. The squamosal is probably considerably larger than in the more generalised ancestor, and the tabular is certainly more reduced than it must have been. Still the type as seen in *Captorhinus* is our best starting-point for tracing the evolution of the temporal region.

In all the Mammal-like reptiles there seems to me no reasonable doubt that the temporal condition has arisen by an opening forming between the postorbital and the squamosal, exactly as figured by Versluys in his "Synapsider Typus I."*. This leaves, when the opening is well formed, a temporal fossa bounded above by the postorbital and squamosal, and below by the jugal and squamosal. In *Diametrodon* and *Gorgonops* and *Galepus* we find this type of fossa, and there is no doubt that, even where as in Cynodonts and some others, the parietal forms part of the temporal border, the condition is a secondary one.

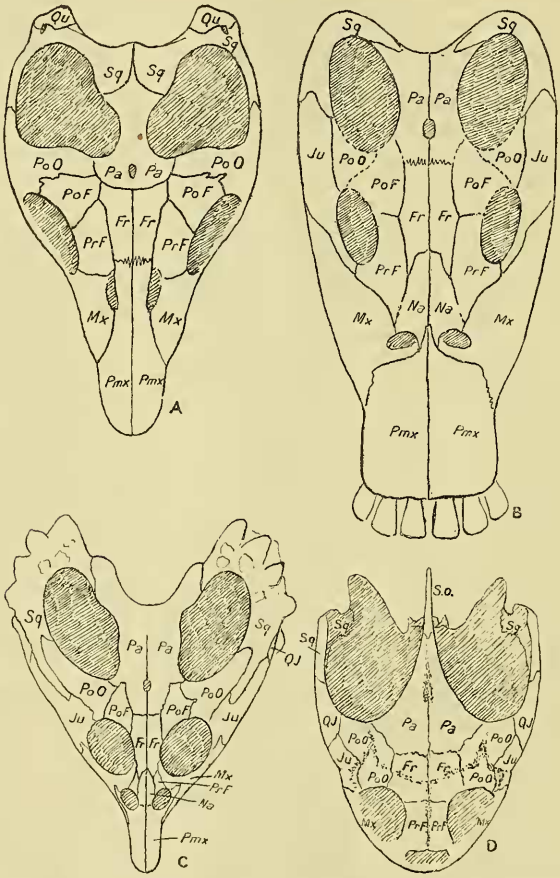
The Mammal-like reptiles with this single lower temporal fossa form a very natural group, to which the name Synapsida has been given by Osborn.

There is another group of reptiles which, having also a single

* Versluys, I. "Ueber den Phylogenie der Schläfenruben und Jochbogen bei den Reptilien," Sitzungsber. der Heidelberger Akad. der Wissenschaften. Heidelberg, 1919.

temporal fossa, have so much superficial resemblance to the Synapsid type that the larger majority of zoologists have concluded that they are really allied to the Mammal-like reptiles. These are the Plesiosaurs. In 1904 I first pointed out that the

Text-figure 2.



Illustrations of temporal regions in a Plesiosaur, Placodonts, and a Chelonian.

A. Skull of *Plesiosaurus macrocephalus* Owen. From skull in Brit. Mus.
B. Skull of *Placodus* sp. From skull in Brit. Mus.
C. Skull of *Placochelys placodonta* Jaekel. After Jaekel.
D. Skull of *Pelomedusa galeata*.

fossa in the Plesiosaurs is really formed between the parietal above and the postorbital and squamosal below, and that it is thus the homologue of the upper fossa in *Sphenodon* and not of

the fossa in the Mammal-like reptiles which really corresponds to the lower fossa in *Sphenodon*. Though this early view of mine has been opposed by Andrews, Williston, Watson, and others, I have never seen reason to alter it, as apart from the superficial resemblance of the upperside of the skull to that of a Therapsid, the fundamental structure of the Plesiosaur is so different from that of the Mammal-like reptiles that I never could agree that the two groups could be at all nearly related. It is with some satisfaction, therefore, that I find Versluys supporting my view, that the fossa in the Plesiosaur has had quite a different origin from that in the Mammal-like reptiles. Versluys makes it his "Synapsider Typus II."

Elsewhere * I am dealing at some length with the question of the affinities of the Plesiosaurs, and the conclusion to which I come is that they are a specialised offshoot from land-reptiles on the line of descent which is leading to the Diapsids, but which have not yet developed a lower temporal fossa.

In near association with the Plesiosaurs must be placed the Placodonts. They are a different specialisation sprung from very similar and closely allied ancestors. There is no essential difference in the temporal regions of the two groups.

The Chelonians are by far the most aberrant and puzzling group among the reptiles. Unfortunately, we know nothing of the ancestry. The earliest-known fossil forms are already typical Chelonians, and help us very little. Among living forms we have great variations in the temporal regions. Some have the region well roofed. Some have practically no roof at all, like the American *Terrapene*. Some have a small roof very deeply encroached on from below, like the Australian Water-Tortoise *Elseya*.

For many years I have adhered to the view, which was also held by Baur, that there is some close relationship between the Chelonia and the Plesiosaurs. Unfortunately, each group is so extremely specialised that hardly any apparent resemblance remains. It is like comparing a Whale and a Bat. The Chelonian and the Plesiosaur has each a remarkable type of shoulder-girdle, nowhere else to be found, and each is merely a modification of the same common type. It is difficult to believe that this remarkable type could have been twice independently evolved. The pelvis, the tarsus, and many points in the skull-structure confirm the affinity.

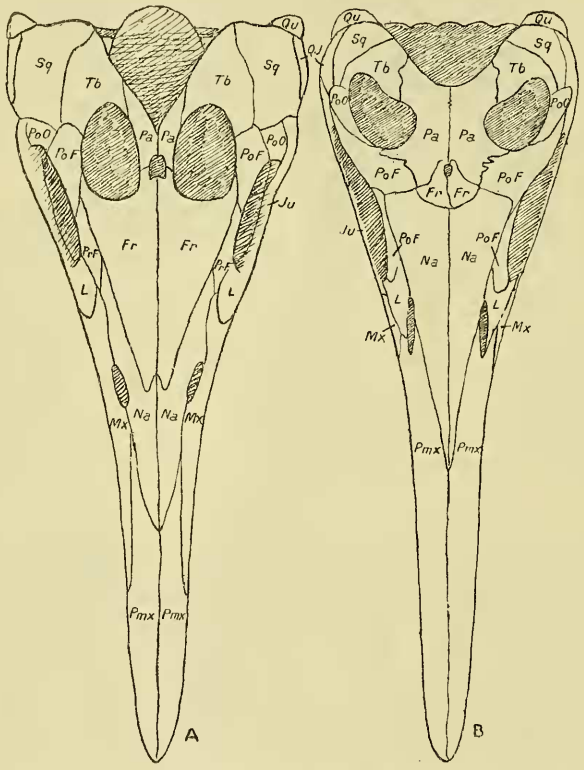
If we assume that the Chelonian is a second remarkable specialisation from a land-type, such as gave rise to the Plesiosaurs by another line, we must conclude that the ancestor of the Chelonian had, like the Plesiosaur, a single temporal fossa, and that the condition now met with in Chelonians has resulted from the loss of the posterior arch. A skull like that of *Trionyx* with its greatly elongated supraoccipital and the squamosal perched on

* Williston Memorial Volume.

the top of the quadrate readily suggests that the posterior squamoso-parietal arch has been pushed out, as it were, by the unusual development of the temporal muscle. And this is confirmed by the fact that occasionally, as in *Hydromedusa*, the posterior arch is still met with.

If we are right in this conclusion, we can hardly resist the further possibility that the Chelonian is quite a near ally of the

Text-figure 3.



A. Skull of *Mixosaurus atavus* Quenst. After v. Huene. ½ nat. size.

B. Skull of *Ichthyosaurus communis* Conyb. After the reconstruction by Sollas, and with the missing squamosal added.

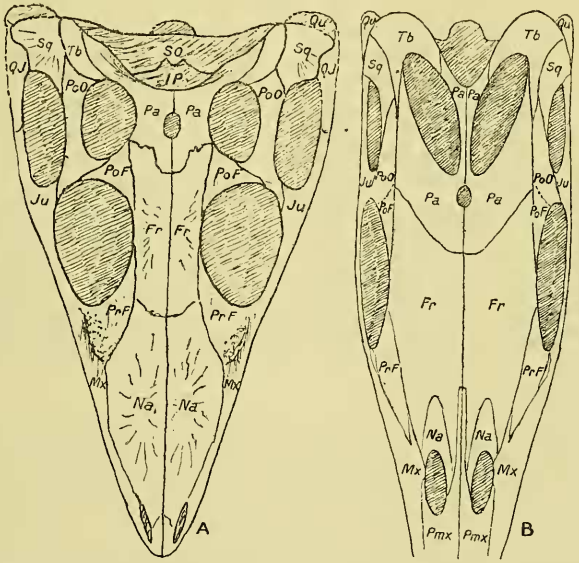
Placodont. Jaekel has shown that *Placochelys* has a turtle-like carapace. Perhaps it may yet turn out that Chelonians are extremely degenerate cousins of the Placodonts.

Another group of aquatic reptiles that have caused some trouble are the Ichthyosaurs. By some they have been held to be aquatic specialisations from a *Sphenodon*-like ancestor. Others

have derived them directly from Cotylosaurs with no near affinity with later forms.

Fortunately, as the result of the work of Sollas and others, we now know the skull fairly well. In the temporal region there is a single supratemporal fossa. Behind and below the fossa are two large membrane-bones, which have given rise to much difference of opinion. By some, the upper bone has been looked upon as the squamosal and the lower called the supratemporal. Most recent writers, however, have identified the lower bone as the squamosal and the upper the supratemporal. I am also

Text-figure 4.



A. Skull of *Youngina capensis* Broom. From the type-skull, further restored from a second specimen. 1½ nat. size.

B. Restoration of greater part of the skull of *Thalattosaurus alexandræ* Merriam. Further restored from Merriam's figure in the light of the later researches of v. Huene.

satisfied that it is the lower bone that is the squamosal. In an extremely specialised skull like that of *Ichthyosaurus* the relations of the bones are manifestly somewhat modified from what was the primitive condition, but it is agreed by most that the two bones are undoubtedly the homologues of the two bones usually found behind the temporal fossa in lizards. These I have elsewhere agreed are the squamosal and tabular. The supratemporal in the Stegocephalians and those Cotylosaurs in which it occurs is apparently merely a roofing-bone with no other important

functions. The tabular is a much more important element. Besides being a bone of the top of the skull, it is also an occipital element with important bony and muscular attachments. The supratemporal is apparently very rarely, if ever, an occipital element at all. For these and other reasons which I am elsewhere giving, I regard the upper element in all the later reptiles in which it occurs as the tabular.

In *Mixosaurus*, *Cymbospondylus*, and *Ichthyosaurus* the back of the temporal fossa and much of the occipital margin is formed by the tabular. The squamosal is situated below it. The relations of the two bones are strikingly similar to those in lizards.

For the discussion of the temporal region in the two-arched reptiles we are very fortunate in having two good skulls of an animal that must be pretty near to the ancestral type. *Youngina capensis*, which I described a few years ago, is too specialised in having a long snout to have itself been the Diapsid ancestor, but it is sufficiently near for all morphological purposes. The temporal region is remarkably interesting. The squamosal is large and lies almost entirely behind the infratemporal fossa. Above the squamosal lies a bone which I think there can be little doubt is the tabular. It is situated between the parietal and the squamosal. The relations of the bones will be best understood from the figure given. Whatever doubt there might have been about the identification of the squamosal in the type-skull is removed by the second skull which I was fortunate in discovering. This second skull, though it lacks the occiput, has the snout well preserved.

The Thalattosauria form a group of very remarkable marine reptiles, which seem to have some affinity with the lizards and *Sphenodon*. Unfortunately, they are very imperfectly known. Merriam, who first described them, gave good figures of the specimens and attempted restorations of the skull. Huene, who has since examined the material, differs from Merriam in the interpretation of some of the parts of the temporal region. The most important difference of opinion is that Huene considers that the squamosal of Merriam is really the supratemporal, and finds the true squamosal in a much smaller bone situated below the larger bone. I am inclined to think that in this Huene is probably right. I give a restoration of the skull, modified from Merriam in the light of Huene's later observations, and with the occiput restored as I think it may have been. If this figure be compared with that of *Youngina* (text-fig. 4, A & B), it will be seen that *Thalattosaurus* is strikingly similar in type, but specialised in a manner curiously parallel to that seen in the primitive Ichthyosaurs *Cymbospondylus* and *Mixosaurus*.

The Lacertilia have given rise to much difference of opinion, not only as to which of the two post-temporal bones is the squamosal, but also as to whether they are really descended from ancestors with two temporal fossæ. It has long seemed to me

that it is impossible to get over the fact that the pterygo-quadrate arch in the lizard is developed exactly as in *Sphenodon*, as I showed many years ago, and that the immediate ancestor of the lizard must have had a fixed quadrate. The lizard still has a lower temporal fossa, which only differs from that of *Sphenodon* or *Youngina* in having become ligamentous when the quadrato-jugal was lost and the quadrate became movable. The two post-temporal bones are manifestly homologous with the two in *Youngina*, and are thus the squamosal and the tabular. Elsewhere * I am giving further evidence in confirmation of this view from the consideration of the facts revealed by the study of the skeletogenesis.

The lizards are interesting, as showing in many cases how the upper temporal fossa of the ancestor may disappear by the approximation of the bones, but outside the Lacertilia I know of no forms where this has manifestly happened.

If the interpretations of the temporal regions given above be agreed to, we can very satisfactorily divide the Reptilia into four subclasses :—

I. We have the primitive types with a roofed temporal region which are usually grouped as Cotylosaurs. The Cotylosauria can hardly be considered as an order. For convenience, every reptile with a roofed skull is at present placed in it, but such a type as *Procolophon* has really very little in common with, say, *Diadectes* or *Pantylus*, and still less with *Seymouria*. If we still wish to keep the roofed forms together we must regard them as forming a subclass and not an order, and Williston's term Anapsida seems a very appropriate one, excluding from it the Chelonia.

II. The Diapsida of Osborn is certainly a very natural group. Starting in the Upper Permian we have the primitive *Eosuchia*, from which we can easily derive all the later two-arched forms, and also the Lacertilia and the Thalattosauria.

III. The Synapsida of Osborn, restricted to the Mammal-like reptiles with a lower temporal fossa, also forms a thoroughly natural third subclass.

IV. We are then left with the Mesosauria, the Ichthyosauria, the Plesiosauria, the Placodontia, and the Chelonia. Can these be placed in a fourth natural subclass ? Very early the reptiles divided into two distinct lines—those that by a lizard-like habit early lost the true coracoid and became possessed of a supra-temporal fossa, and those that by a more Mammal-like habit retained both coracoid and precoracoid and developed an infra-temporal fossa. Until the Upper Permian times, when the two-arched reptiles make their appearance, all reptiles belonged to the Synapsida, the Anapsida, or to this other proposed subclass. Unfortunately, very few of the land-types are known. Doubtless they became early extinct in the struggle with the

* Williston Memorial Volume.

better-equipped two-arched forms, and we can at present only examine the very specialised aquatic modifications that survived. *Broomia* is probably the only well-known land-form. *Araeosceles* is probably also a member of the group, but so very early that it still retains the true coracoid. In no other is a true coracoid known. The Mesosaurs are very early aquatic modifications. The Ichthyosaurs are much later aquatic forms. The Plesiosaurs and Placodonts and Chelonians are, I believe, all descended from land forms closely similar to *Youngina*, but with only the upper temporal fossa developed.

This group of primitive lizard-like forms, which had only the upper temporal fossa developed, and their aquatic descendants the Mesosaurs, the Ichthyosaurs, the Plesiosaurs, and Placodonts, together with the very highly specialised Chelonians, which I consider to be all related, I proposed to unite in a fourth subclass, which I suggest may be called the ANOMAPSIDA.